



Phylogeny and evolution of habitat preference in *Goniurosaurus* (Squamata: Eublepharidae) and their correlation with karst and granite-stream-adapted ecomorphologies in species groups from Vietnam

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Abstract

Maximum likelihood (ML) and Bayesian inference (BI) analyses using two mitochondrial (16S and *cyt b*) and two nuclear (CMOS and RAG1) genes and 103 specimens recovered the first phylogenies of all 23 extant species of *Goniurosaurus*. The analyses strongly supported the recognition of four monophyletic species groups with identical inter-specific relationships within the *kuroiwae*, *lichtenfelderi*, and *yingdeensis* groups but discordant topologies at some nodes within the *lunii* group. Both analyses recovered a polyphyletic *G. luii* with respect to *G. kadoorieorum*, and owing to the lack of diagnostic characters in the latter, it is considered a junior synonym of *G. luii*. A stochastic character mapping analysis of karst versus non-karst habitat preference suggested that karstic landscapes may have played a major role in the evolution and diversification of *Goniurosaurus*. A karst habitat preference is marginally supported as the most probable ancestral condition for *Goniurosaurus* as well as for the *kuroiwae*, *lunii*, and *yingdeensis* groups. However, a non-karst habitat preference is marginally supported as the most probable ancestral condition for the *lichtenfelderi* group. Multivariate and univariate ecomorphological analyses of the karst-adapted *G. catbaensis*, *G. huuliensis*, and *G. luii* of the *lunii* group and the granite-stream-adapted *G. lichtenfelderi* of the *lichtenfelderi* group demonstrated that their markedly statistically different body shapes may be an adaptive response that contributes to habitat partitioning in areas of northern Vietnam where they are nearly sympatric.

Keywords

Asia, stochastic character mapping, systematics, synonymy, tiger geckos

Introduction

Eublepharid geckos of the genus *Goniurosaurus* Barbour, 1908 comprise 23 saxicolous specialists (Uetz et al. 2021) that extend from the Ryukyu Archipelago in Japan, southward through East Asia to northern Vietnam. *Goniurosaurus* is a well-defined monophyletic group (Grismer 1988) comprised of four monophyletic species groups: the *kuroiwae* group containing six species endemic to the Ryukyu Archipelago, Japan; the *lichtenfelderi* group with five species from insular and mainland China and northern Vietnam; the *luii* group with eight species from northern Vietnam, some of its offshore islands, and southern China; and the *yingdeensis* group consisting of four species from southern China (Kurita et al. 2008; Nguyen et al. 2009; Nguyen 2011; Wang et al. 2013; Honda and Ota 2017; Liang et al. 2018; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). Apart from these species, *Goniurosaurus sinensis* Zhou, Peng, Huo and Yuan, 2019 is likely a junior synonym of another species from Hainan Island, China and not included herein (Qi et al. in progress). Phylogenetic relationships within *Goniurosaurus* have never been strongly supported nor consistent among different studies (e.g. Wang et al. 2013; Liang et al. 2018; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). This protracted state of discordance results, in part, from researchers focusing on different species groups as opposed to the

entire genus, as well as using different genes or different combinations of genes with varying combinations of ingroup and outgroup species—all variables that bear significantly on tree construction (Wiens 1998; Zwickl et al. 2002; Heath et al. 2008; Wiens and Morrill 2011; Wainwright and Price 2016). The most commonly used genetic markers have been the mitochondrial genes 12S and 16S rRNA and cytochrome *b* (*cyt b*). Liang et al. (2018) were the first to address the challenges of properly aligning rRNA (Pyron et al. 2013) and constructed a well-supported mito-nuclear data set using 16S, *cyt b*, and the nuclear genes oocyte maturation factor MOS (CMOS), and recombination activating 1 (RAG1). Zhu et al. (2020b) also used this mito-nuclear combination, but examined only relationships within the *lichtenfelderi* group.

In an effort to continue building a more global understanding of the phylogenetic relationships within *Goniurosaurus*, we expanded the mito-nuclear data set of Liang et al. (2018) to include 103 individuals as opposed to 31 and 23 as opposed to 17 species, which for the first time, includes all extant species of the genus (Table 1). We used this phylogeny in a stochastic character state mapping (SCM) analysis (Revell 2012) of habitat preference to explore the role karstic landscapes may have played in the evolution and diversification of *Goniurosaurus* and if

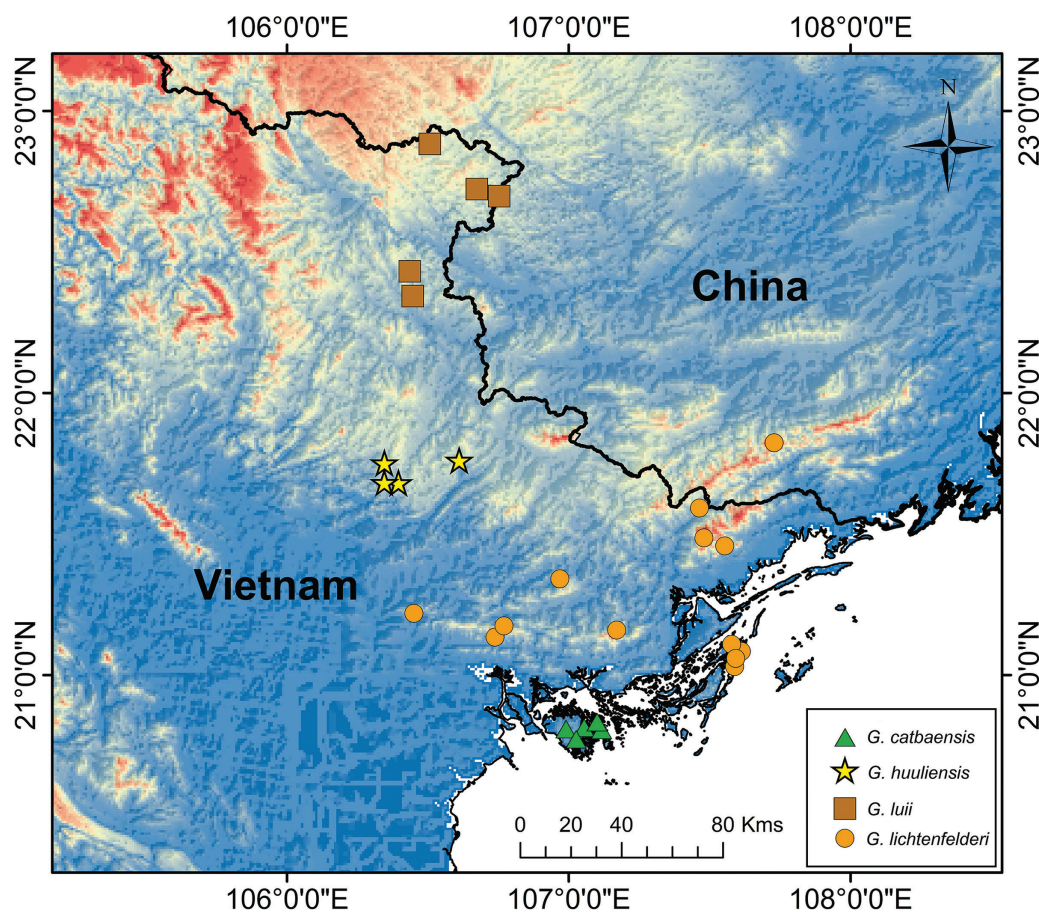


Figure 1. Distribution of the four recorded species of *Goniurosaurus* in Vietnam and China used in the ecomorphological analysis.

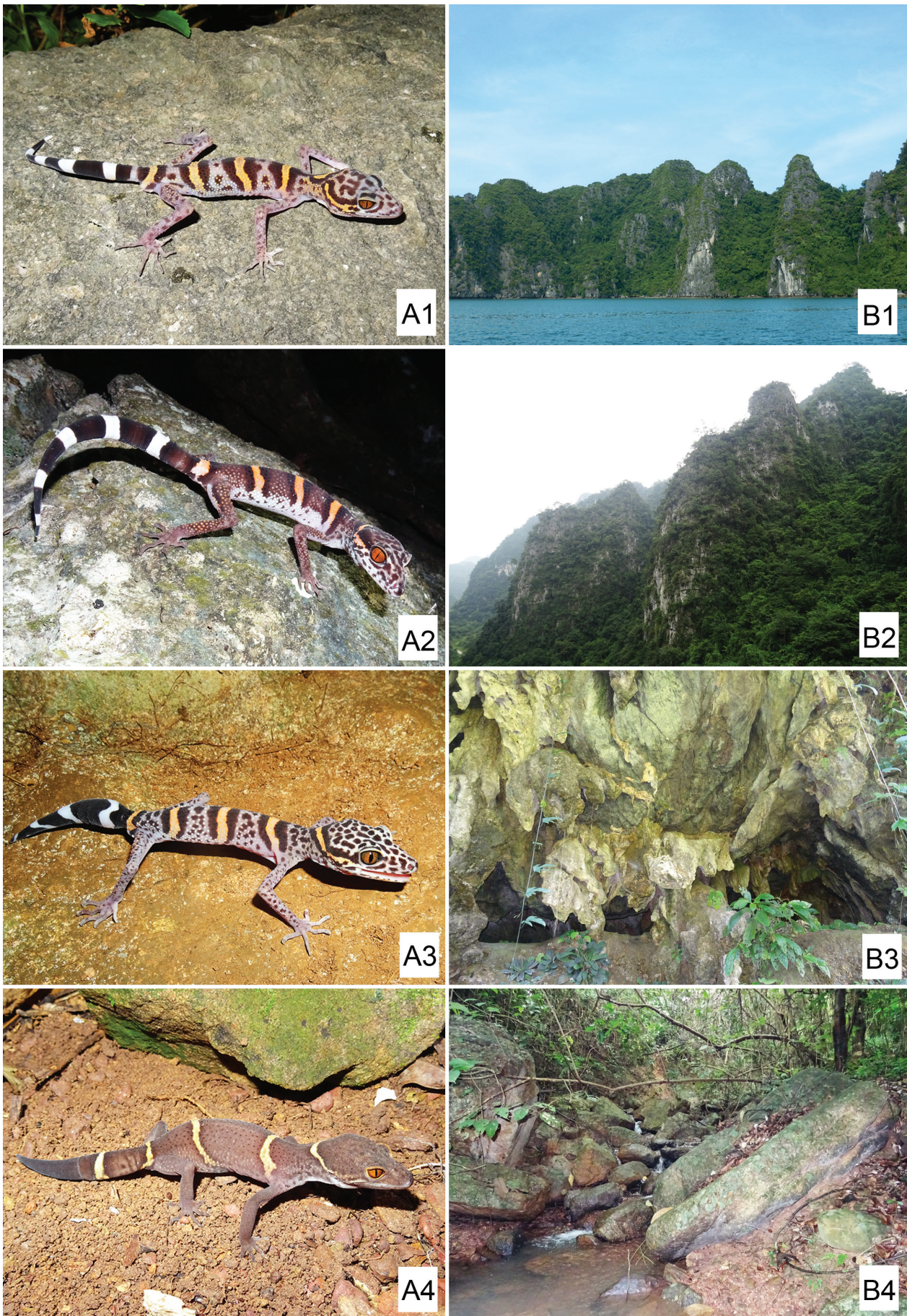


Figure 2. A1–A3. Photos of karst-adapted species (*Goniurosaurus catbaensis*, *G. huuliensis*, and *G. luii*, respectively), A4. Granite-stream-adapted species (*G. lichtenfelderi*), B1 – B3. Karst habitats of the *luii* group, B4. Granite-stream habitat of the *lichtenfelderi* group. Photos by Hai Ngoc Ngo.

Table 1. Species and GenBank accession numbers of the sequenced specimens used herein.

Species/Specimen	16s	cytb	CMOS	RAG1
<i>Goniurosaurus araneus</i>	AB308460			
<i>G. araneus</i> ECNU-V0008	MT533259			
<i>G. araneus</i> JFBM15830			HQ426537	HQ426286
<i>G. bawanglingensis</i> BL-RBZ-021	MH247190	MH247201	MH247212	MH247223
<i>G. bawanglingensis</i> BL-RBZ-022	MH247191	MH247202	MH247213	MH247224
<i>G. bawanglingensis</i> BL-RBZ-023	MH247192	MH247203	MH247214	MH247225
<i>G. bawanglingensis</i> BL-RBZ-024	MH247193	MH247204	MH247215	MH247226
<i>G. bawanglingensis</i> SYS r002162	MT995758	MT995773		
<i>G. catbaensis</i> G33	MW741550	MW650944		
<i>G. catbaensis</i> G34	MW741551	MW650945		
<i>G. catbaensis</i> G35		MW650946		
<i>G. catbaensis</i> MHNG 2699.49	EU499389			
<i>G. gezhi</i> ECNU-V0038	MT533260			
<i>G. gezhi</i> ECNU-V0040	MT533261			
<i>G. gezhi</i> ECNU-V0042	MT533262			
<i>G. gezhi</i> ECNU-V0046	MT533263			
<i>G. gezhi</i> ECNU-V0047	MT533264			
<i>G. gollum</i> SYS r002420	MT995784	MT995787	MW727559	MW727594
<i>G. gollum</i> SYS r002421	MT995785	MT995788	MW727560	MW727595
<i>G. gollum</i> SYS r002422	MT995786	MT995789	MW727561	MW727596
<i>G. hainanensis</i> BL-RBZ-041	MH247194	MH247205	MH247216	MH247227
<i>G. hainanensis</i> BL-RBZ-042	MH247195	MH247206	MH247217	MH247228
<i>G. hainanensis</i> SYS r000349	KC765080			
<i>G. hainanensis</i> JK1	AB308458			
<i>G. huuliensis</i> Gohu	AB853453	AB853479		
<i>G. huuliensis</i> G21		MW650936		
<i>G. huuliensis</i> G23		MW650937		
<i>G. huuliensis</i> G24		MW650938		
<i>G. kadoorieorum</i> ECNU-V0058	MT533258			
<i>G. kadoorieorum</i> ECNU-V0060	MT533265			
<i>G. kadoorieorum</i> ECNU-V0061	MT533266			
<i>G. kuroiwaie</i> Goku1 Northern Okinawa	AB853448	AB853473		
<i>G. kuroiwaie</i> Goku2 Southern Okinawa	AB853445			
<i>G. kuroiwaie</i> Goor1 Southern Okinawa	AB853446	AB853467		
<i>G. kwanghua</i> ECNU-V0003	MK782788	MK782782	MK782776	MK782770
<i>G. kwanghua</i> ECNU-V0004	MK782789	MK782783	MK782777	MK782771
<i>G. kwanghua</i> ECNU-V0005	MK782790	MK782784	MK782778	MK782772
<i>G. kwangsiensis</i> ECNU-V0009	MK782786	MK782780	MK782774	MK782768
<i>G. liboensis</i> SYS r000217	KC900230			
<i>G. lichtenfelderi</i> ECNU-V0007	MK782785	MK782779	MK782773	MK782767
<i>G. lichtenfelderi</i> IEBR 3692	JF799756			
<i>G. luii</i> ECNU-V0012	MK782787	MK782781	MK782775	MK782769
<i>G. luii</i> Golu2			EF081254	
<i>G. luii</i> Golu3	AB853452	AB853478		
<i>G. luii</i> SYSr 000255	KC765083			
<i>G. luii</i> SYSr 000256	KC765084			
<i>G. luii</i> ZFMK 87057	EU499391			
<i>G. luii</i> TG00795				HQ426287
<i>G. orientalis</i> Goku3	AB853446			
<i>G. orientalis</i> Goor2	AB853443	AB853461		
<i>G. orientalis</i> Goor3		AB853462		
<i>G. sengokui</i> Gose1	AB853444	AB853463		
<i>G. sengokui</i> Gose2		AB853464		
<i>G. sengokui</i> KUZ 62087			HQ876393	
<i>G. splendens</i> Gosp1	AB853451	AB853477		
<i>G. splendens</i> Gosp2	AB853449			
<i>G. splendens</i> Gosp3	AB853450			

Species/Specimen	16s	cytb	CMOS	RAG1
<i>G. toyamai</i> Goto1	AB853447	AB853468		
<i>G. toyamai</i> Goto2		AB853469		
<i>G. varius</i> SYS r002331	MT995754	MT995769	MW727556	MW727590
<i>G. varius</i> SYS r002332	MT995755	MT995770		
<i>G. varius</i> SYS r002333	MT995753	MT995768		
<i>G. varius</i> SYS r002362	MT995756	MT995771	MW727557	MW727592
<i>G. varius</i> SYS r002363	MT995757	MT995772	MW727558	MW727593
<i>G. varius</i> SYS r002485	MW721828	MW727532	MW727562	MW727597
<i>G. varius</i> SYS r002486	MW721829	MW727533	MW727563	MW727598
<i>G. yamashinae</i> Goya1	AB853442	AB853460		
<i>G. yamashinae</i> Goya2	AB853441	AB853459		
<i>G. yamashinae</i> Goya3		AB853458		
<i>G. yingdeensis</i> Field number DYA01	MW721830	MW727534	MW727574	MW727605
<i>G. yingdeensis</i> Field number DYA02	MW721831	MW727535	MW727575	MW727606
<i>G. yingdeensis</i> Field number HS01	MW721832	MW727536	MW727576	MW727607
<i>G. yingdeensis</i> Field number HS02	MW721833	MW727537	MW727577	MW727608
<i>G. yingdeensis</i> Field number LT01	MW721834	MW727538	MW727580	MW727611
<i>G. yingdeensis</i> Field number LT02	MW721835	MW727539	MW727581	MW727612
<i>G. yingdeensis</i> SYS r000549	KC765082			
<i>G. yingdeensis</i> SYS r000550	KC900231			
<i>G. yingdeensis</i> SYS r001271	MT995759	MT995774	MW727547	
<i>G. yingdeensis</i> SYS r001272	MT995760	MT995775	MW727548	
<i>G. yingdeensis</i> SYS r001493	MT995761	MT995776	MW727551	
<i>G. yingdeensis</i> SYS r0002115	MT995762	MT995777		
<i>G. zhelongi</i> Field number HW01	MW721838	MW727540	MW727578	MW727609
<i>G. zhelongi</i> Field number HW02	MW721839	MW727541	MW727579	MW727610
<i>G. zhelongi</i> Field number MDA01	MW721836	MW727542	MW727582	MW727613
<i>G. zhelongi</i> Field number MDA02	MW721837	MW727543	MW727583	MW727614
<i>G. zhelongi</i> Field number TZ01	MW721840	MW727544	MW727584	MW727615
<i>G. zhelongi</i> Field number TZ02	MW721841	MW727545	MW727585	MW727616
<i>G. zhelongi</i> SYS r000816	KJ423105	MT995778	MW727570	
<i>G. zhelongi</i> SYS r001491	MT995763	MT995779	MW727549	
<i>G. zhelongi</i> SYS r001492	MT995764	MT995780	MW727550	
<i>G. zhelongi</i> SYS r002108	MT995765	MT995781		
<i>G. zhoui</i> BL-RBZ-001	MH247196	MH247207	MH247218	MH247229
<i>G. zhoui</i> BL-RBZ-004	MH247197	MH247208	MH247219	MH247230
<i>G. zhoui</i> BL-RBZ-006	MH247198	MH247209	MH247220	MH247231
<i>G. zhoui</i> BL-RBZ-007	MH247199	MH247210	MH247221	MH247232
<i>G. zhoui</i> BL-RBZ-008	MH247200			
<i>G. zhoui</i> SYS r002213	MT995766	MT995782	MW727553	
<i>G. zhoui</i> SYS r002214	MT995767	MT995783	MW727554	
<i>Eublepharis macularius</i>	AB853454	AB853480		

habitat preference coevolved with ecomorphology in near sympatric species of the *luiti* and *lichtenfelderi* groups in Vietnam (Ngo et al. 2021; Figs. 1, 2).

Materials and methods

Genetic data and phylogenetic analyses

Genomic DNA was extracted from muscle tissue samples, using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. Primers used for 16S were r16S-5L

(5'- GGTMMYGCCTGCCAGTG -3') and 16Sbr-H (5'- CCGGTCTGAACTCAGATCACGT-3') (Palumbi et al. 1991), for *cyt b* the primers were L14731 (5'- TG-GTCTGAAAAACCATTGTTG-3') (Honda et al. 2014) and H15149m (5'- GCMCCTCAGAAGKATATTTGY-CCTCA-3') (Chambers and MacAvoy 1999), for CMOS the primers were FU-F (5'- TTTGGTTCKGTCTACAA-GGCTAC -3') and FU-R (5'- AGGGAACATCCAAAG-TCTCCAAT -3') (Gamble et al., 2008), and for RAG1 the primers were R13 (5'- TCTGAATGGAAATTCAG-CTGTT -3') and R18 (5'- GATGCTGCCTCGGTCGG-CCACCTTT -3') (Groth and Barrowclough 1999). The PCR procedure was performed with an initial denaturation at 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min, followed by a final

extension at 72 °C for 10 min (Liang et al. 2018). PCR products were purified with spin columns and then sequenced with forward primers using BigDye Terminator Cycle Sequencing Kit as per the guidelines on an ABI Prism 3730 automated DNA sequencer by Shanghai Majorbio Bio-pharm Technology Co., Ltd.

We constructed Maximum Likelihood (ML), Bayesian Inference (BI), and Bayesian Evolutionary Analysis by Sampling Trees (BEAST) phylogenetic trees using a concatenated data set composed of 3070 base pairs (bp) of the mitochondrial genes, 16S (633 bp) and *cyt b* (1075 bp), and the nuclear genes, CMOS (472 bp) and RAG1 (890), from 103 specimens of 23 species of *Goniurosaurus* with varying degrees of sequence coverage across the samples (Table 1). Concatenation followed the comparison of separate gene trees to confirm there were no major discordances. One species, *Eublepharis macularius*, served as an outgroup (Grismer 1988; Jonniaux and Kumazawa 2008) to root the trees. Sequence data and GenBank accession numbers are listed in Table 1.

A Maximum likelihood (ML) analysis partitioned by gene was implemented using the IQ-TREE web-server (Nguyen et al. 2015; Trifinopoulos et al. 2016) preceded by the selection of substitution models using TIM2+F+I+G4 for 16S and *cyt b* and HKY+F for CMOS and RAG1. To avoid over parameterization, protein coding genes were not partitioned by codon. One-thousand bootstrap pseudoreplicates via the ultrafast bootstrap (UFB: Hoang et al. 2018) approximation algorithm were employed, and nodes having UFB values of 95 and above were considered strongly supported (Minh et al. 2013). We considered nodes with values of 90–94 as well-supported. A Bayesian inference (BI) analysis was carried out in MrBayes 3.2.3. (Ronquist et al. 2012) on XSEDE using the CIPRES Science Gateway (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010) employing default priors and models of evolution that most closely approximated those selected by the BIC and used in the ML analysis. Two independent Markov chain Monte Carlo (MCMC) analyses for each data set were performed—each with four chains, three hot and one cold. The MCMC simulations ran for 100 million generations. Trees were sampled every 10,000 generations, and the first 10% of the trees from each run from each data set were discarded as burn-in. The parameter files from both runs were checked in Tracer v1.6 (Rambaut et al. 2014) to ensure that convergence and stationarity of all parameters had effective sample sizes (ESS) well-above 200. Post-burn-in sampled trees from each respective run were combined and 50% majority-rule consensus trees were constructed. Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered highly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002). We considered nodes with values of 0.90–0.94 as well-supported.

An input file was constructed in Bayesian Evolutionary Analysis Utility (BEAUti) v. 2.4.6 using a relaxed lognormal clock with unlinked site models, linked trees and clock models, and a Yule prior and run in BEAST on CIPRES (Cyberinfrastructure for Phylogenetic Research;

Miller et al. 2010). bModelTest was used to numerically integrate over the uncertainty of substitution models of each gene while simultaneously estimating phylogeny using Markov chain Monte Carlo (MCMC). MCMC chains were run for 100,000,000 generations and logged every 10,000 generations. The BEAST log file was visualized in Tracer v. 1.6.0 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) were well-above 200 for all parameters. A Maximum clade credibility tree using mean heights at the nodes was generated using TreeAnnotator v.1.8.0 (Rambaut and Drummond 2014) with a burn-in of 1000 trees (10%). Nodes with BPPs of 0.95 and above were considered strongly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002). We considered nodes with values of 0.90–0.94 as well-supported.

Ancestral state reconstruction

The BEAST tree was converted to newick format and pruned using the *drop.tip()* command (Paradis and Schliep 2018) in the R package ape [v.3.4.3] to include only the earliest diverged individual of each species. Habitat preference (karst or non-karst; see below) was mapped onto the tree using SCM implemented in the R package Phytools (Revell 2012) in order to derive probability estimates of the ancestral states at each node. A transition rate matrix was identified that best fit the data by comparing the corrected Akaike Information Criterion (AICc) values in the R package ape (Paradis and Schliep 2018). Three transition rate models were considered: a 2-parameter model having different rates for every transition type (the ARD model); a single-parameter model with equal forward and reverse rates between states (the symmetrical rates SYM model); and a single rate parameter model that assumes equal rates among all transitions (ER). Lastly, an MCMC approach was used to sample the most probable 1000 trait histories from the posterior using the *make.simmap()* command and then summarized them using the *summary()* command.

The coding of habitat preference for each species was determined from the literature and field observations of the authors (Table 2). A species' habitat preference was coded as "karst" if it had a strong association with karstic habitats. Many such species may range into forested areas or even other rock types (granite or volcanic) if nearby but their densities are much greater in karstic areas. A species was coded as "non-karst" if detected only in forested areas or forested areas with other rock types (e.g. granite). These species never show any strong preference for karstic microhabitats even if such habitats exist within their range.

Morphological data and analyses

An ecomorphological analysis was conducted using four of the five recorded species from Vietnam (Grismer et al. 1999; Vu et al. 2006; Orlov et al. 2008; Ziegler et al. 2008; Nguyen et al. 2009; Nguyen 2011; Orlov et al.

Table 2. Habitat preferences of the species of *Goniurosaurus*.

Species	1° habitat	2° habitat	Source
kuroiwaie group			
<i>G. splendens</i>	karst	forest	Nakamura and Ueno (1963), H. Ota pers. comm., L. Grismer pers. obs.
<i>G. toyamai</i>	forest		H. Ota pers. comm.
<i>G. kuroiwaie</i> North	forest		H. Ota pers. comm., L. Grismer pers. obs.,
<i>G. kuroiwaie</i> South	karst	forest	Nakamura and Ueno (1963), H. Ota pers. comm., L. Grismer pers. obs.
<i>G. yamashinae</i>	karst	forest	H. Ota pers. comm., L. Grismer pers. obs.,
<i>G. sengokui</i>	karst	forest	Werner et al. (2004), H. Ota pers. comm.
<i>G. orientalis</i>	karst		H. Ota pers. comm.
yingdeensis group			
<i>G. gollum</i>	karst		Qi et al. (2020a)
<i>G. yingdeensis</i>	karst	granite	Wang et al. (2010), S. Qi pers. obs.
<i>G. zhelongi</i>	karst	granite	S. Qi, pers. obs., Wang et al. (2014)
<i>G. varius</i>	karst		Qi et al. (2020b)
lichtenfelderi group			
<i>G. bawanglingensis</i>	granite	karst	Grismer et al. (2002), Orlov et al. (2008)
<i>G. zhoui</i>	karst	granite	Zhou et al. (2018), S. Qi pers. obs.
<i>G. kwanghua</i>	karst	granite	Zhu et al. (2020)
<i>G. lichtenfelderi</i>	granite		Orlov et al. (2008)
<i>G. hainanensis</i>	granite	volcanic	S. Qi pers. obs., L. Grismer pers. obs.
lunii group			
<i>G. catbaensis</i>	karst		Ziegler et al. (2008), Ngo et al. (2019a)
<i>G. gezhi</i>	karst		Zhu et al. (2020)
<i>G. araneus</i>	karst		Grismer et al. (1999)
<i>G. kadoorieorum</i>	karst		Yang and Chan (2015)
<i>G. huuliensis</i>	karst		Orlov et al. (2008)
<i>G. luii</i>	karst		Grismer et al. (1999), Vu et al. (2006)
<i>G. liboensis</i>	karst		Wang et al. (2013)
<i>G. kwangsiensis</i>	karst		Yang and Chan (2015)

2020) for which there existed a substantially large morphometric data set (Ngo et al. 2021): the karst-adapted *G. catbaensis* Ziegler, Nguyen, Schmitz, Stenke, and Rösler, 2008, *G. huuliensis* Orlov, Ryabov, Nguyen, Nguyen, and Ho, 2008, and *G. luii* Grismer, Viets, and Boyle, 1999 of the *lunii* group and the granite stream-adapted *G. lichtenfelderi* (Mocquard, 1897) of the *lichtenfelderi* group (Figs. 1, 2). A total of 486 live individuals and 54 museum specimens of four species were examined for morphological data, comprising 194 individuals of *G. catbaensis* (21 juveniles, 93 females, and 80 males), 80 individuals of *G. huuliensis* (two juveniles, 46 females, and 32 males), and 88 individuals of *G. luii* (11 juveniles, 43 females, and 34 males) of the *lunii* species group and 178 individuals of *G. lichtenfelderi* (14 juveniles, 72 females, and 92 males) of the *lichtenfelderi* group.

Measurements were taken with dial calipers to the nearest 0.1 mm on the right side of each individual. Abbreviations are as follows: snout-vent length (SVL), from tip of snout to vent; axilla to groin length (AG), from posterior edge of forelimb insertion to anterior edge of hind limb insertion; maximum body width (BW), greatest width of torso, taken at level of midbody; maximum body height (BH), from dorsal surface of body to belly; inter-narial distance (ID), distance between nares; head length (HL), from the tip of snout to posterior edge of occiput; maximum head width (HW); cheek height (CH), from

posterior edge of labial to top of head at parietal region; interorbital distance (IO), distance between posteriormost points of eyes; diameter of auditory meatus (AD); snout to eye distance (SL), measured from tip of snout to anteriormost point of eye; diameter of eye (ED), greatest diameter of eye; eye to ear distance (EE), from posterior margin of eye to posterior margin of ear; forelimb length (FLL), from axilla to the tip of the fourth finger; hind limb length (HLL), from groin to the tip of the fourth toe. To remove potential effects of allometry, size was adjusted using the following equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000)—accessible in the R package *GroupStruct* (available at <https://github.com/chankinonn/GroupStruct>). The morphometrics of each species were adjusted separately and then concatenated so as not to conflate intra- with interspecific variation (Reists 1986). All data were then scaled to their standard deviation to insure they were analyzed on the basis of correlation and not covariance and were log-transformed to insure they were normally distributed.

An analysis of variance (ANOVA) was performed on a data set coded for species to search for the presence of statistically significant mean differences ($p < 0.05$)

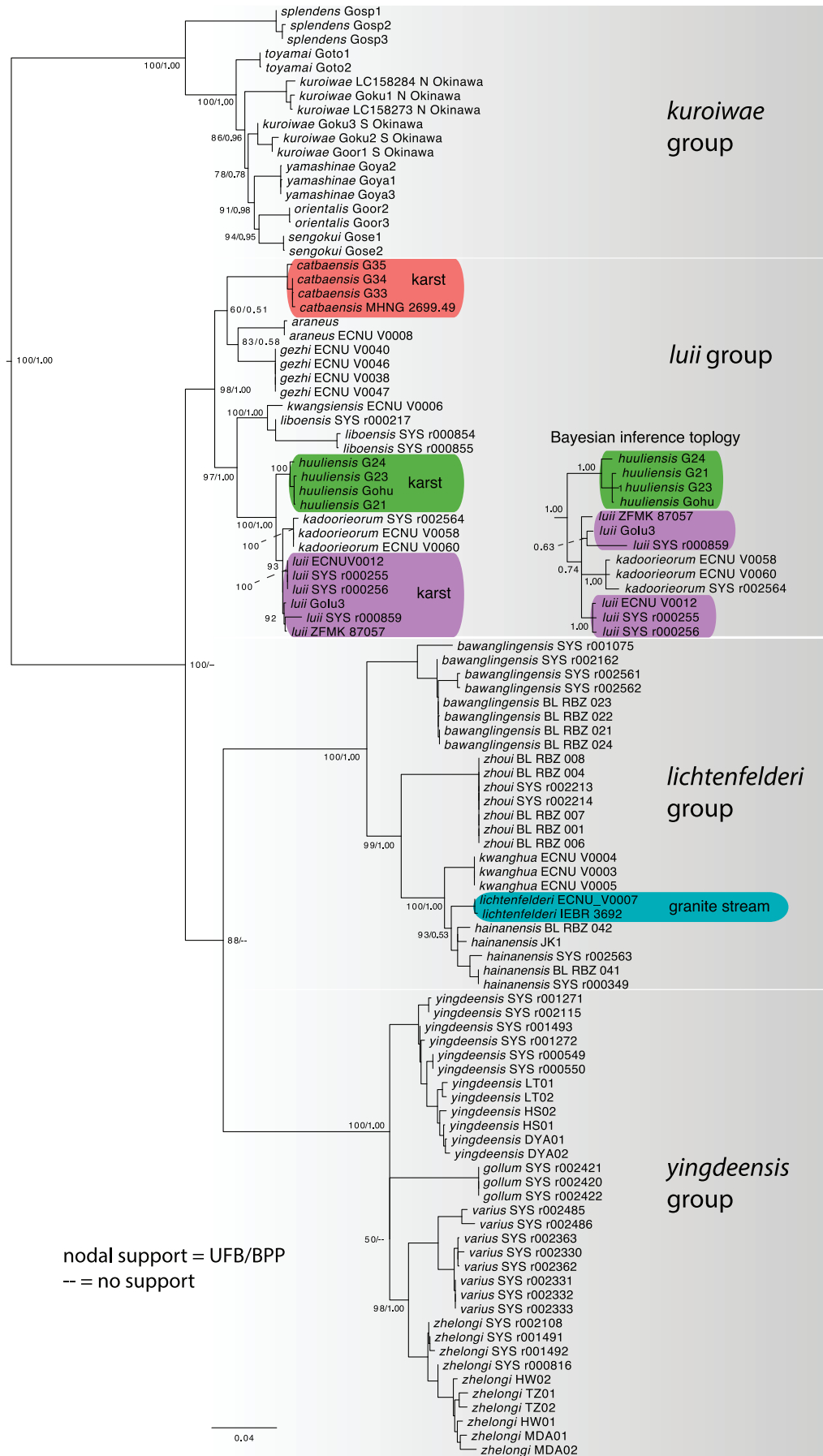


Figure 3. Mito-nuclear maximum likelihood topology with ultrafast bootstrap values (UFB) and Bayesian posterior probabilities (BPP) at the nodes. All species except *Goniurosaurus luii* had strong nodal support (100/1.00) for their monophyly. The inset in the *luii* species group is a section of the BI analysis showing the non-monophyly of *G. luii* with respect to *G. kadoorieorum*. Colored species are those used in the ecomorphological analyses.

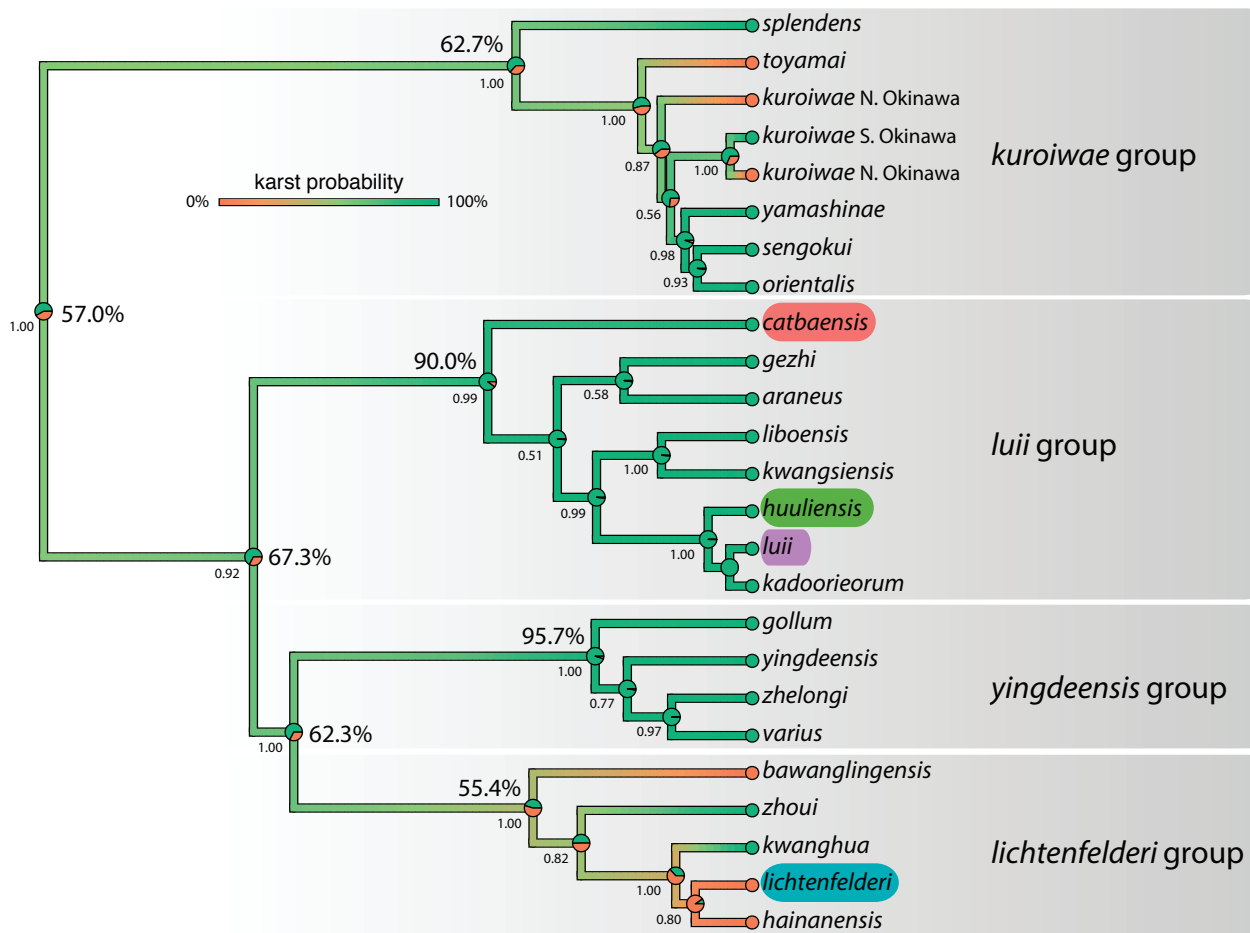


Figure 4. Stochastic character map of karst and non-karst habitat preferences on a BEAST topology. Percentages at the nodes are the probability of the ancestral habitat preference. Numbers at the nodes are BPP values. Colored species are those used in the eco-morphological analyses.

among characters across the selected subset of species in the *luyi* and *lichtenfelderi* groups. Character means bearing statistical differences among species were subjected to a TukeyHSD test to ascertain which species pairs differed significantly from each other for those particular characters. A Student *t*-test was also performed on a second data set coded for only habitat preference (karst versus non-karst) to search for the presence of statistically significant mean differences ($p < 0.05$) among the same subsets of species coded for habitat. Violin plots with inserted boxplots were generated in order to visualize the range, frequency, mean, 50% quartile, and degree of differences between the dependent variables for both data sets bearing statistically different mean values.

The morphospacial clustering of the two separate data sets (species and habitat preference) were visualized using principal component analysis (PCA) along the ordination of the first two principal components (PC) using the Adegenet package in R (Jombart et al. 2010) and implemented by the *prcomp()* command. The data were log-transformed prior to analysis in order to normalize their distribution so as to ensure characters with very large or very low values could not over-leverage the results owing to intervariable nonlinearity. All statistical analyses were performed using R.3.1.2 (R Core Team 2018).

Results

Phylogenetic relationships

The ML, BI, and BEAST analyses recovered strong nodal support (UFB 98–100/BPP 1.00) for the monophyly of all four species groups with the *kuroiwaie* group being the strongly supported (100/1.00) sister group to the remaining three groups (Fig. 3). The ML analysis weakly recovered (88) the *lichtenfelderi* and *yingdeensis* groups as sister lineages but the BEAST analysis recovered this relationship with strong support (1.00; Fig. 4). The BI analysis recovered the *luyi* and *yingdeensis* groups as sister lineages, although the support is so low (0.51), the three groups effectively form a polytomy. The ML and BI analyses recovered the identical inter-specific relationships within the species groups but discordant relationships with the BEAST analysis regarding the *luyi* group. The ML and BI analyses recovered a poorly supported (*G. catbaensis* (*G. araneus*, *G. gezhi*)) clade but the BEAST analysis recovered *G. catbaensis* as the strongly supported (0.99) sister species to the remainder of the *luyi* group species (Figs. 3, 4, respectively). All analyses recovered a polyphyletic *Goniurosaurus luyi* with respect to *G. kadoorieorum* (not shown in the pruned tree of Fig. 4).

Table 3. Difference, lower and upper ranges, and adjusted *p* values of statistically significant mean differences between species pairs for each character based on ANOVA and subsequent TukeyHSD analyses.

	difference	lower range	upper range	<i>p</i> adjusted
axilla-groin (AG)				
<i>huuliensis-catbaensis</i>	0.095633573	0.072292064	0.118975082	3.37E-10
<i>lichtenfelderi-catbaensis</i>	-0.075967576	-0.094200659	-0.057734493	3.37E-10
<i>luii-catbaensis</i>	-0.029676257	-0.05225407	-0.007098445	0.004206065
<i>lichtenfelderi-huuliensis</i>	-0.171601149	-0.195246969	-0.14795533	3.37E-10
<i>luii-huuliensis</i>	-0.12530983	-0.152447204	-0.098172456	3.37E-10
<i>luii-lichtenfelderi</i>	0.046291319	0.023399042	0.069183596	1.60E-06
body width (BW)				
<i>huuliensis-catbaensis</i>	0.106179184	0.066412755	0.145945613	4.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.083314667	-0.123599543	-0.043029791	8.67E-07
<i>luii-huuliensis</i>	-0.121548632	-0.167781995	-0.075315269	5.34E-10
body height (BH)				
<i>huuliensis-catbaensis</i>	0.094637915	0.046801122	0.142474708	2.84E-06
<i>lichtenfelderi-huuliensis</i>	-0.07317021	-0.121630666	-0.024709755	0.000647886
<i>luii-huuliensis</i>	-0.125013692	-0.180629845	-0.069397539	7.11E-08
<i>luii-lichtenfelderi</i>	-0.051843482	-0.098759605	-0.004927359	0.02359844
internarial distance (ID)				
<i>lichtenfelderi-catbaensis</i>	-0.082396274	-0.105742691	-0.059049857	3.37E-10
<i>luii-catbaensis</i>	-0.076638786	-0.105548379	-0.047729192	4.74E-10
<i>lichtenfelderi-huuliensis</i>	-0.096677642	-0.126954757	-0.066400527	3.37E-10
<i>luii-huuliensis</i>	-0.090920154	-0.125668004	-0.056172303	5.78E-10
head length (HL)				
<i>huuliensis-catbaensis</i>	0.075818967	0.058801575	0.092836359	3.37E-10
<i>lichtenfelderi-catbaensis</i>	-0.162875997	-0.176169033	-0.149582961	3.37E-10
<i>luii-catbaensis</i>	-0.029098886	-0.045559496	-0.012638276	3.82E-05
<i>lichtenfelderi-huuliensis</i>	-0.238694964	-0.255934217	-0.221455712	3.37E-10
<i>luii-huuliensis</i>	-0.104917853	-0.124702663	-0.085133043	3.37E-10
<i>luii-lichtenfelderi</i>	0.133777111	0.117087238	0.150466985	3.37E-10
head width (HW)				
<i>huuliensis-catbaensis</i>	0.036775074	0.019138869	0.05441128	6.89E-07
<i>lichtenfelderi-catbaensis</i>	-0.158637831	-0.172414249	-0.144861413	3.37E-10
<i>luii-catbaensis</i>	-0.065002064	-0.082061241	-0.047942887	3.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.195412905	-0.213279039	-0.177546772	3.37E-10
<i>luii-huuliensis</i>	-0.101777138	-0.122281395	-0.081272881	3.37E-10
<i>luii-lichtenfelderi</i>	0.093635767	0.07633899	0.110932545	3.37E-10
head height (HH)				
<i>huuliensis-catbaensis</i>	0.108413032	0.073172094	0.143653969	3.37E-10
<i>lichtenfelderi-catbaensis</i>	-0.032237965	-0.059766217	-0.004709713	0.014142658
<i>lichtenfelderi-huuliensis</i>	-0.140650997	-0.176351381	-0.104950613	3.37E-10
<i>luii-huuliensis</i>	-0.14002168	-0.180993602	-0.099049757	3.37E-10
cheek height (CH)				
<i>huuliensis-catbaensis</i>	0.069595379	0.028246161	0.110944597	0.000101199
<i>lichtenfelderi-catbaensis</i>	-0.14807373	-0.180373429	-0.11577403	3.37E-10
<i>luii-catbaensis</i>	-0.057345812	-0.09734215	-0.017349473	0.001381599
<i>lichtenfelderi-huuliensis</i>	-0.217669109	-0.259557409	-0.175780808	3.37E-10
<i>luii-huuliensis</i>	-0.126941191	-0.175014741	-0.078867641	5.00E-10
<i>luii-lichtenfelderi</i>	0.090727918	0.050174509	0.131281326	8.27E-08
interorbital distance (ID)				
<i>huuliensis-catbaensis</i>	0.05692565	0.034698839	0.079152461	9.29E-10
<i>lichtenfelderi-catbaensis</i>	-0.211451872	-0.228814215	-0.194089528	3.37E-10
<i>luii-catbaensis</i>	-0.03636425	-0.057863835	-0.014864664	9.22E-05
<i>lichtenfelderi-huuliensis</i>	-0.268377522	-0.29089411	-0.245860933	3.37E-10
<i>luii-huuliensis</i>	-0.093289899	-0.1191313	-0.067448499	3.37E-10
<i>luii-lichtenfelderi</i>	0.175087622	0.15328859	0.196886655	3.37E-10
snout length (SL)				
<i>huuliensis-catbaensis</i>	0.108547374	0.083797596	0.133297152	3.37E-10

<i>lichtenfelderi-catbaensis</i>	-0.20706889	-0.226402034	-0.187735746	3.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.315616264	-0.340688712	-0.290543816	3.37E-10
<i>luii-huuliensis</i>	-0.125435452	-0.154210112	-0.096660792	3.37E-10
<i>luii-lichtenfelderi</i>	0.190180812	0.16590737	0.214454254	3.37E-10
ear diameter (ED)				
<i>huuliensis-catbaensis</i>	-0.137477526	-0.199198043	-0.075757008	9.51E-08
<i>lichtenfelderi-catbaensis</i>	-0.338691314	-0.386903935	-0.290478693	3.37E-10
<i>luii-catbaensis</i>	-0.365692271	-0.425393393	-0.305991149	3.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.201213788	-0.263738975	-0.138688602	3.37E-10
<i>luii-huuliensis</i>	-0.228214745	-0.299972435	-0.156457055	3.37E-10
eye to ear distance (EE)				
<i>huuliensis-catbaensis</i>	0.085091637	0.059731157	0.110452117	3.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.06878479	-0.094475902	-0.043093678	4.25E-10
<i>luii-huuliensis</i>	-0.101777804	-0.131262479	-0.072293128	3.37E-10
<i>luii-lichtenfelderi</i>	-0.032993014	-0.057865404	-0.008120623	0.00377334
eye diameter (ED)				
<i>huuliensis-catbaensis</i>	0.085091637	0.059731157	0.110452117	3.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.06878479	-0.094475902	-0.043093678	4.25E-10
<i>luii-huuliensis</i>	-0.101777804	-0.131262479	-0.072293128	3.37E-10
<i>luii-lichtenfelderi</i>	-0.032993014	-0.057865404	-0.008120623	0.00377334
forelimb length (FLL)				
<i>huuliensis-catbaensis</i>	-0.137477526	-0.199198043	-0.075757008	9.51E-08
<i>lichtenfelderi-catbaensis</i>	-0.338691314	-0.386903935	-0.290478693	3.37E-10
<i>luii-catbaensis</i>	-0.365692271	-0.425393393	-0.305991149	3.37E-10
<i>lichtenfelderi-huuliensis</i>	-0.201213788	-0.263738975	-0.138688602	3.37E-10
<i>luii-huuliensis</i>	-0.228214745	-0.299972435	-0.156457055	3.37E-10
hindlimb length (HLL)				
<i>huuliensis-catbaensis</i>	-0.137477526	-0.199198043	-0.075757008	9.51E-08

The mito-nuclear data set of Liang et al. (2018) differed from all the above analyses in that their ML and BI analyses (79/0.99) placed the *yingdeensis* group as the sister group to a sister lineage comprised of the *luii* group and *lichtenfelderi* group (87/1.00).

Ancestral state reconstruction

The AICc scores for the three transition rate models of the SCM analysis were ARD = 34.547134 and SYM and ER = 32.099451. The SCM analysis using either the SYM or ER model suggests that a karst habitat preference is the most probable ancestral condition for *Goniurosaurus* (57.0% probability), the *kuroiwa* group (62.7%), the *luii* group (90.0%), and the *yingdeensis* group (95.7%; Fig. 4). The probable ancestral condition for the *lichtenfelderi* group is non-karst (55.4%). The karst habitat preference of *G. kwanghua* and *G. zhoui* of the *lichtenfelderi* group is considered to have evolved independently given that the ancestral condition of the *lichtenfelderi* group and that of the most recent common ancestor of the sister species *G. lichtenfelderi* and *G. hainanensis* was not karst-adapted (Fig. 4).

Ecomorphology

In both the species and habitat preference PCA analyses, PC1 accounted for 49.1% of the variation in the data

set and loaded most heavily for limb length (FLL and HLL), snout length (SL), eye diameter (ED), interorbital distance (IO), head width (HW), and head length (HL). PC2 accounted for an additional 13.3% of the variation and loaded most heavily for body width (BW) and body height (BH) (Figs. 5, 6; Table 4).

The PCA analysis of the karst-adapted *Goniurosaurus catbaensis*, *G. huuliensis*, and *G. luii* of the *luii* group demonstrates that their body shapes greatly overlap in morphospace despite there being several slight, but statistically significant mean differences among them (Fig. 5; Table 3). Additionally, none of the plots of the karst-adapted species overlap with that of the granite stream-adapted species *G. lichtenfelderi* along the ordination of PC1.

The PCA analysis using habitat preference as the dependent variable among the four species, showed that the karst-adapted and granite-stream-adapted species plot separately as before along taxonomic lines and that collectively, the former have significantly longer axilla-groin lengths (AG); longer, wider, and thicker heads (HL, HW, and CH); longer snouts (SL); longer limbs (FLL and HLL); wider interorbital distances (IO); larger eyes (ED) and larger ear openings (AD) (Fig. 6). Many of these characters—longer head and snout, larger eyes, longer trunk, longer limbs—occur in many other distantly related karst-adapted species of *Cyrtodactylus* (Grismer et al. 2016a, 2020b; Kaatz et al. 2021; Nielsen and Oliver 2017), indicating that these are convergent adaptations to a karstic life style within and between the gekkotan families.

Table 4. Summary statistics and principal component analysis scores for the mensural characters for *Goniurosaurus catbaensis*, *G. huiliensis*, *G. luyi*, and *G. lichtenfelderi*. Abbreviations are listed in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14
Standard deviation	2.62151	1.36659	1.03962	0.92238	0.82762	0.77172	0.71922	0.62534	0.54279	0.51042	0.44460	0.42745	0.41145	0.18664
Proportion of variance	0.49088	0.1334	0.0772	0.06077	0.04893	0.04254	0.03695	0.02793	0.02104	0.01861	0.01412	0.01305	0.01209	0.00249
Cumulative proportion	0.49088	0.62428	0.70148	0.76225	0.81118	0.85371	0.89066	0.9186	0.93964	0.95825	0.97237	0.98542	0.99751	1
Eigenvalue	6.87232	1.86758	1.08081	0.85079	0.68496	0.59554	0.51728	0.39105	0.29462	0.26053	0.19767	0.18272	0.16929	0.03483
AG	-0.24490	-0.08424	0.09672	0.10058	-0.56138	0.67337	-0.35690	0.01987	-0.04902	0.07718	-0.08231	0.03497	-0.02384	0.01371
BW	-0.04928	-0.61441	-0.07471	0.28744	-0.08051	-0.01832	0.20859	-0.63240	-0.03995	-0.19837	0.15593	-0.11090	0.06221	0.01347
BH	-0.04819	-0.61109	-0.04352	0.29637	0.08259	-0.06845	0.04189	0.71074	0.07724	0.07219	-0.03719	-0.04417	-0.03405	0.02105
NID	-0.18533	-0.11312	0.64606	0.12685	0.26270	-0.29150	-0.55437	-0.15934	-0.06520	0.16090	-0.04518	0.00367	0.01346	-0.01680
HL	-0.34765	0.02673	-0.05102	-0.02271	0.00465	-0.10546	-0.03065	0.01183	0.02638	-0.32873	0.17358	0.23473	-0.81798	0.00137
HW	-0.33156	-0.06751	-0.07095	-0.08475	0.05312	-0.03718	0.30763	-0.17678	0.01022	0.48788	-0.67604	-0.04173	-0.21464	0.01521
CH	-0.22962	-0.07645	-0.23672	-0.12992	0.73588	0.52586	-0.13009	-0.06367	0.04671	0.02514	0.139	0.0252	0.08193	-0.0003
IO2	-0.34276	0.00113	-0.05114	0.03079	-0.01618	-0.12015	0.10256	0.06796	-0.38288	-0.23806	-0.14615	0.67256	0.40575	-0.08672
SE	-0.32091	0.01885	-0.14557	-0.08578	-0.10147	-0.18206	-0.18393	-0.02718	0.77823	-0.28404	-0.17039	-0.03379	0.27124	-0.00567
ED	-0.32467	0.19657	0.01794	0.11714	0.06087	-0.00844	0.0395	0.12818	-0.36952	-0.45307	-0.20533	-0.65522	0.08037	-0.01989
EE	-0.08674	-0.33966	0.34954	-0.81367	-0.09736	0.04251	0.1902	0.08589	-0.05072	-0.11731	0.09913	-0.09141	0.05499	0.02214
AD	-0.19445	0.23327	0.54515	0.30447	0.06568	0.23322	0.5704	0.05955	0.28325	0.01759	0.2077	0.05512	0.05956	0.0013
FLL	-0.35278	0.08503	-0.16262	-0.01768	-0.10677	-0.18636	-0.00643	0.02061	-0.09402	0.28874	0.3664	-0.07982	0.12433	0.73937
HLL	-0.34892	0.04532	-0.17931	-0.04073	-0.1368	-0.17019	0.00654	0.02352	-0.04871	0.36988	0.42336	-0.16275	0.07515	-0.666

Discussion

Geckos in general are particularly well-adapted to karstic landscapes (see Luu et al. 2016; Grismer et al. 2014, 2020a, 2021 and references therein; Google Scholar search using key words “karst” and “Gekkonidae”) and *Goniurosaurus* is no exception, being that 19 of its 23 species (83%) occupy karstic habitats (Grismer et al. 1994, 1999; Orlov et al. 2008; Ziegler et al. 2008; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Ngo et al. 2019a; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). It is clear that karstic landscapes have played a significant role in the evolution and diversification of *Goniurosaurus* being that it is the probable ancestral habitat preference for the genus and three of the four species groups. Even the ancestor of the non-karst adapted ancestor of the *lichtenfelderi* group was karst-adapted (Fig. 4). Furthermore, within the species groups, the limited data herein would suggest that the karst-adapted species are specialized, range-restricted endemics (Grismer et al. 1994, 1999; Orlov et al. 2008; Ziegler et al. 2008; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Ngo et al. 2019a; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b). With the exception of *G. lichtenfelderi*, all the non-karst-adapted species are restricted to islands in the Ryukyu Archipelago (*kuroi-wae* group) or Hainan Island (*lichtenfelderi* group). It may be that the absence of competition and/or predators in these insular habitats widened the fundamental niches of their ancestors and allowed some species to become more generalized in their habitat preference, which should be tested using new techniques combining phylogenetic history, character evolution, and ecological reconstruction programs.

Systematics of the *luyi* group

The ML and BI analyses of Liang et al. (2018) and the BEAST analysis herein (Fig. 4) recovered *Goniurosaurus catbaensis* as the strongly supported sister species to the remainder of the *luyi* group. Whereas the ML and BI analysis herein, recovered *G. catbaensis* as the very poorly supported (60/0.51) sister species of the *G. araneus* plus *G. gezhi* clade (Fig. 3). Given that three of the five analyses strongly supported the former relationship and two analyses poorly supported the latter, we prefer the placement of *G. catbaensis* as the sister species to the remainder of the *luyi* group (Fig. 4). Given the very low nodal support of the latter, it essentially renders that portion of the tree a polytomy and as such, does not effectively contradict the strongly supported sister species position of *G. catbaensis* in the other trees.

Goniurosaurus kadoorieorum of the *luyi* group (represented by only 16S) is nested within *G. luyi* in

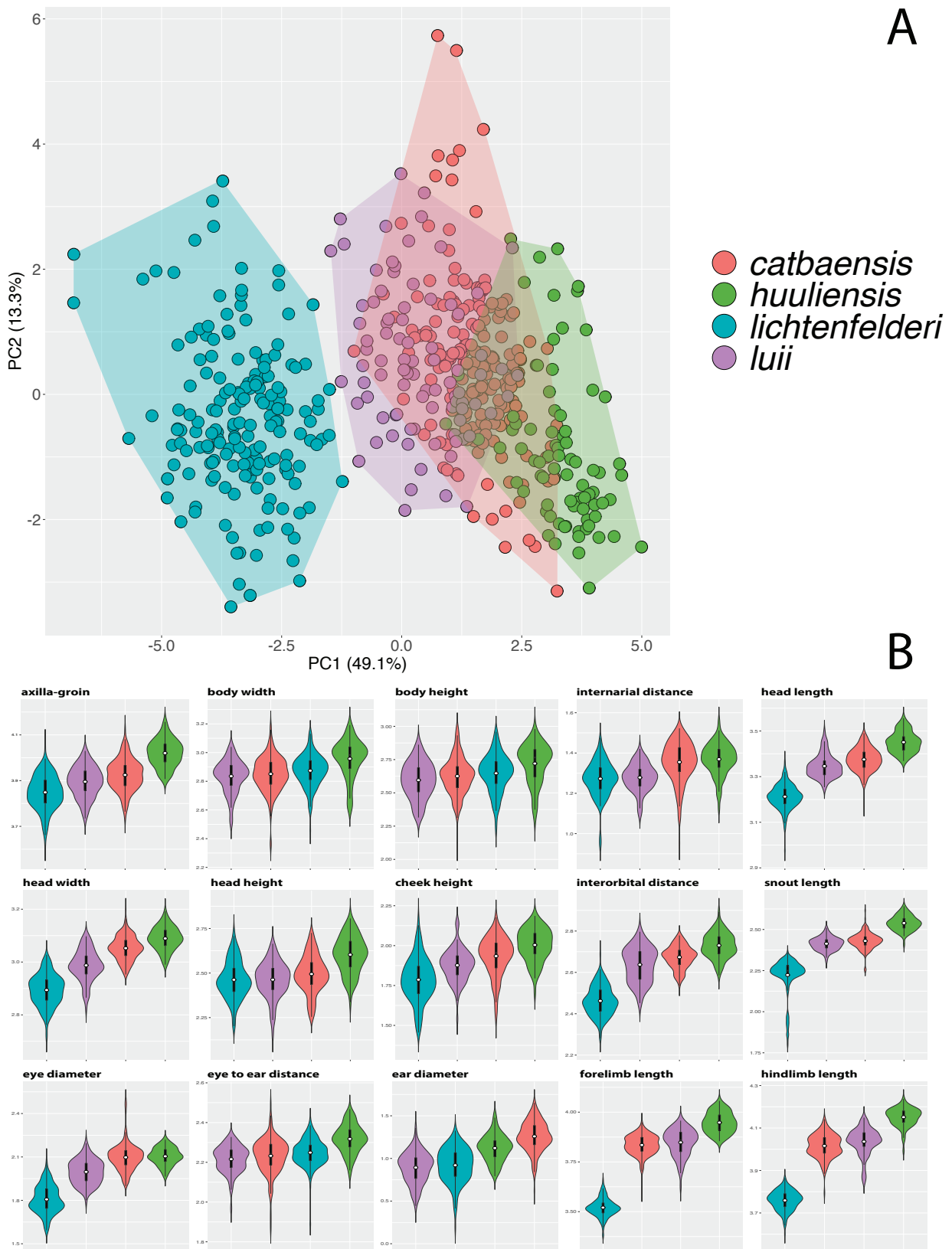


Figure 5. A. Principal component analysis of the karst-adapted species *G. catbaensis*, *G. huuliensis*, and *G. luei* of the *luei* group and the granite-stream-adapted *G. lichtenfelderi* of the *lichtenfelderi* group. B. Violin plots overlain with box plots showing the range, frequency, mean (white dot), and 50% quartile (black rectangle) of the size-adjusted morphometric characters.

both the ML and BI analyses, rendering *G. luei* polyphyletic (Fig. 3). The same relationship was recovered in the 16S phylogeny of Zhu et al. (2020a). This, and the lack of diagnostic characters separating *G. kadoorieorum* from

G. luei (Yang and Chan 2015; Ngo et al. 2016), indicates the two species should be considered conspecific and as such, *G. kadoorieorum* Yang and Chan, 2015 is relegated here to a junior synonym of *G. luei* Grismer, Viets, and

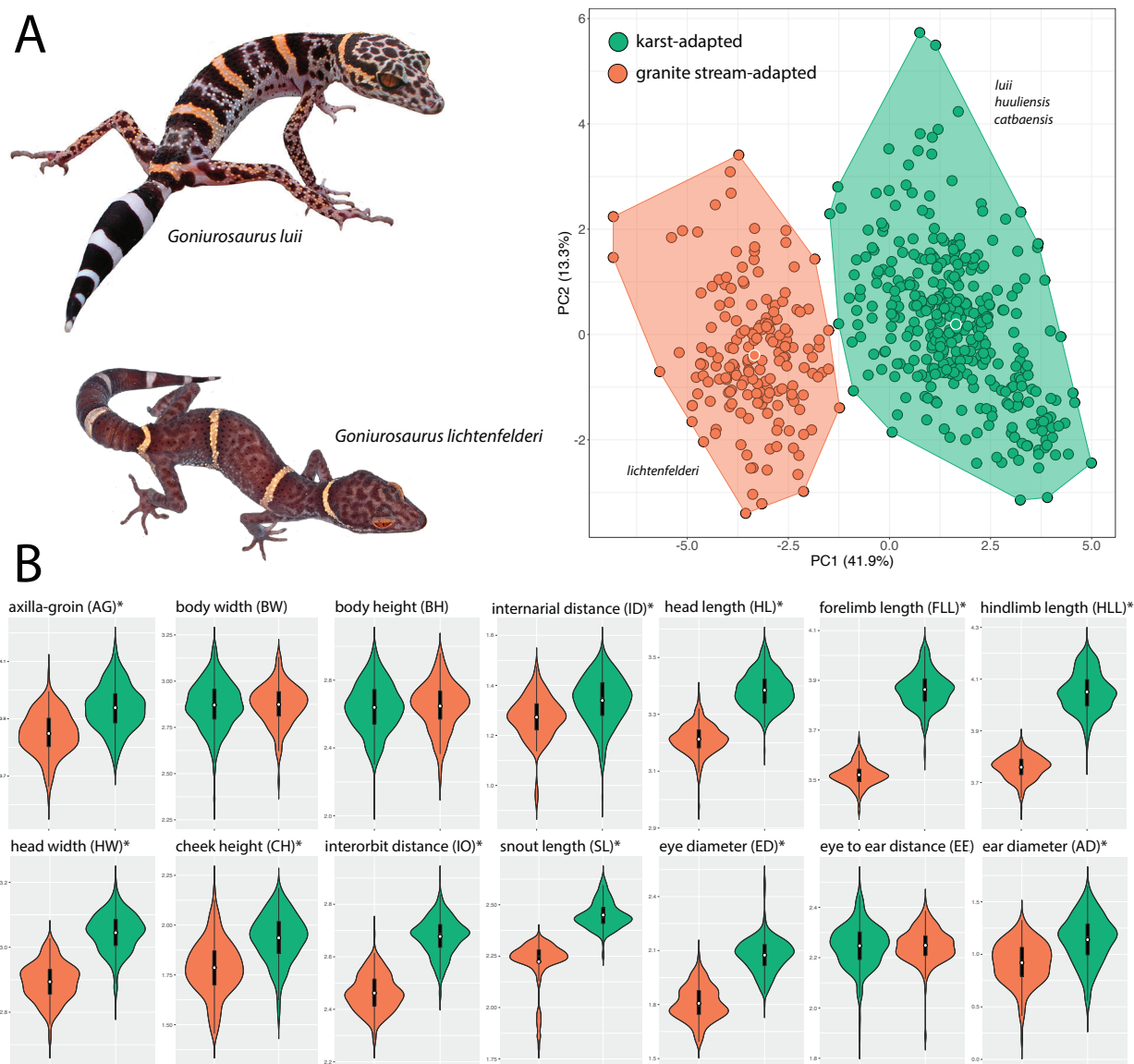


Figure 6. A. Principal component analysis using karst habitat preference and granite stream habitat preference as the dependent variables for *G. catbaensis*, *G. huuliensis*, and *G. luei* of the *luei* group and *G. lichtenfelderi* of the *lichtenfelderi* group. B. Violin plots overlain with box plots showing the range, frequency, mean (white dot), and 50% quartile (black rectangle) of the size-adjusted morphometric characters. Asterisks denote characters bearing statistically significant mean differences between the karst and granite-stream-adapted species based on student *t*-tests. Upper photo from Vuu et al. (2008). Lower photo from Hai Ngoc Ngo.

Boyle, 1999. In all analyses, *G. huuliensis* is consistently recovered as the sister species to *G. luei sensu lato* and its species status is not questioned (Figs. 3, 4).

Conservation

Wide-ranging more inclusive studies pertaining to ecosystems management are becoming commonplace in light of climate change and widespread habitat destruction. Such studies reconcile data from a broad range of disciplines in order to address issues that may bear on ecosystems management. Foundational to many of these studies is a basic understanding of species ecology and habitat preference—correlated here with ecomorphology (Cabral et al. 2009; Harfoot et al. 2014). Baseline information on habitat and microhabitat requirements of any species are

paramount to understanding how they interact with, and navigate through, their environment (e.g. Grant and Grant 2008; Greene 2005; Losos 2010) and as such, the contextualization of ecosystem management may ultimately turn on these simple points (Meiri 2018; Sinervo et al. 2010).

Integrating the phylogenetic patterns of biodiversity and the morphological adaptations of habitat preference that, in part, underpin species radiations, can fundamentally contribute to conservation management programs (Grismer et al. 2020a, 2021; Erwin 1991; Vane-Wright et al. 1991; Williams et al. 1991; Vázquez and Gittleman 1998; Moritz et al. 2000; Forest et al. 2007; Sgro et al. 2010; Harvey et al. 2011; Rolland et al. 2012; Winter et al. 2012; Shaffer et al. 2015; Beaumont and Wang 2019; Fay et al. 2019; Holderegger et al. 2019)—especially in the karstic regions of northern Vietnam where anthropogenic impact is degrading the habitat and reducing the

density of localized populations of *Goniurosaurus* (Ngo et al. 2019b). Northern Vietnam and many of its offshore islands in the Gulf of Tonkin, harbor large areas of fragmented karstic habitats scattered across their landscapes (Cerrano et al. 2006; Do 2001, 2014; Luo et al. 2016; Ngo et al. 2019a) that are inhabited by an exceptionally large number of endemic plants and animals (Do 2001; Sterling et al. 2006; Clements et al. 2008; Luo et al. 2016; von Oheimb et al. 2017). The obligate restriction of many species to fragmented karstic environments—such as all species of the *luiti* and *yingdeensis* groups—functionally transforms these environments into habitat islands (Clements et al. 2006, 2008; von Oheimb et al. 2017), which in some cases, bear an unprecedented degree of range-restricted endemism (e.g. Sgro et al 2012; Harvey et al. 2011; Grismer et al. 2018a, 2021).

Unfortunately, *Goniurosaurus* species are particularly attractive (Fig. 2) and over-harvested for the illegal pet trade (Stuart et al. 2006; Yang and Chan 2015; Ngo et al. 2019b). This is an additional threat to these range-restricted endemics from imperiled karstic environments (Grismer et al. 1997; Orlov et al. 2008; Ziegler et al. 2008; Nakamura et al. 2014; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Ngo et al. 2019a; Qi et al. 2020a,b; Zhu et al. 2020a,b). In fact, in areas of China and Vietnam, many populations have suffered huge declines in numbers, or even extirpation at some localities, due to the illegal commercial pet trade (Stuart et al. 2006; Yang and Chan 2015; Ngo et al. 2019b, 2021). We hope that this study will bring more clarity to the plight of this genus and continue to serve ongoing conservation and management programs.

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References

- Barbour T (1908) Some new reptiles and amphibians. *Bulletin of the Museum of Comparative Zoology* 51: 315–325.
- Beaumont M, Wang J (2019) Conservation genetics. In: Balding D, Moltke I, Marioni J (eds), *Handbook of Statistical Genomics*: fourth edition. Wiley Online Library. <https://doi.org/10.1002/9781119487845.ch16>
- Cabral JS, Wiegand K, Kreft H (2009) Interactions between ecological, evolutionary and environmental processes unveil complex dynamics of insular plant diversity. *Journal of Biogeography* 46: 1582–1597. <https://doi.org/10.1111/jbi.13606>
- Cerrano C, Azzini F, Bavestrello G, Calcinaï B, Pansini M, Sarti M, Thung D (2006) Marine lakes of karst islands in Ha Long Bay (Vietnam). *Chemistry and Ecology* 22: 489–500
- Chambers G, MacAvoy, ES (1999) *Molecular Genetic Analysis of Hybridization*. Department of Conservation, Wellington, 29 pp.
- Clements R, Sodhi NS, Schilthuizen M, Ng PKL (2006) Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *BioScience* 56: 733–742. [https://doi.org/10.1641/0006-3568\(2006\)56\[733:LKOSAI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.CO;2)
- Clements R, Ng PKL, Lu XX, Ambu S, Schilthuizen M, Bradshaw CJA (2008) Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. *Biological Conservation* 141: 2751–2764. <https://doi.org/10.1016/j.biocon.2008.08.011>
- Do T (2001) Characteristics of karst ecosystems of Vietnam and their vulnerability to human impact. *Acta Geologica Sinica (English Edition)* 75: 325–329. <https://doi.org/10.1111/j.1755-6724.2001.tb00539.x>
- Do TC (2014) Distinctive features of the property of Cat Ba archipelago, Vietnam. *Journal of Earth Science and Engineering* 4: 271–283. <https://doi.org/10.17265/2159-581X/2014.05.003>
- Erwin TL (1991) An evolutionary basis for conservation strategies. *Science* 253: 750–752. <https://doi.org/10.1126/science.253.5021.750>
- Fay MF, Gargiulo R, Viruel J (2019) The present and future for population genetics, species boundaries, biogeography and conservation. *Botanical Journal of the Linnean Society* 191: 299–304. <https://doi.org/10.1093/botlinnean/boz076>
- Forest F, Grenyer R, Rouget M, Davies JT, Cowling RM, Faith DP, Balmford A, Manning JC, Proches S, van der Bank M, Reeves G, Hedderson TAJ, Savolainen V (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445: 757–760. <https://doi.org/10.1038/nature05587>
- Grant PR, Grant BR (2008) How and why species multiply: the radiation of Darwin’s finches. Princeton University Press, Princeton, NJ.
- Greene HW (2005) Organisms in nature as a central focus for biology. *Trends in Ecology and Evolution* 20: 23–27.
- Grismer LL (1988) The phylogeny, taxonomy, classification, and biogeography of eublepharid geckos (Reptilia: Squamata). In “Phylogenetic Relationships of the Lizard Families” Ed by Estes R, Pregill, G Stanford University Press, California, pp 369–469.
- Grismer LL, Ota H, Tanaka S (1994) Phylogeny, classification, and biogeography of *Goniurosaurus kuroiwa* (Squamata: Eublepharidae) from the Ryukyu Archipelago, Japan, with description of a new subspecies. *Zoological Science* 11: 319–335.
- Grismer LL, Viets BE, Boyle LJ (1999) Two new continental species of *Goniurosaurus* (Squamata: Eublepharidae) with a phylogeny and evolutionary classification of the genus. *Journal of Herpetology* 33: 382–393. <http://dx.doi.org/10.2307/1565635>

- Grismer LL, Wood PL Jr., Le MD, Quah ESH, Grismer JL (2020a) Evolution of habitat preference in species of Bent-toed geckos (Genus *Cyrtodactylus* Gray, 1827) with a discussion of karst habitat conservation. *Ecology and Evolution* 2020;00: 1–14.
- Grismer LL, Chan KO, Oaks JR, Neang T, Lang S, Murdoch ML, Stuart BL, Grismer JL (2020b) A new insular species of the *Cyrtodactylus intermedius* (Squamata: Gekkonidae) group from Cambodia with a discussion of habitat preference and ecomorphology. *Zootaxa* 4830: 75–102. <https://doi.org/10.11646/zootaxa.4830.1.3>
- Grismer LL, Wood Jr, PL, Thura MK, Zin T, Quah ESH, Murdoch ML, Grismer MS, Lin A, Kyaw H, Ngwe L (2018a) Twelve new species of *Cyrtodactylus* Gray (Squamata: Gekkonidae) from isolated limestone habitats in east-central and southern Myanmar demonstrate high localized diversity and unprecedented microendemism. *Zoological Journal of the Linnean Society* 182: 862–959. <http://dx.doi.org/10.1093/zoolinnean/zlx057>
- Grismer LL, Wood Jr, PL, Anuar S, Grismer MS, Muin MA, Davis HR, Aguilar C, Klaback R, Cobos AJ, Aowphol A, Sites Jr, J (2016a) Two new Bent-toed Geckos of the *Cyrtodactylus pulchellus* complex from Peninsular Malaysia and multiple instances of convergent adaptation to limestone forest ecosystems. *Zootaxa* 4105: 401–429. <https://doi.org/10.11646/zootaxa.4105.5.1>
- Grismer LL, Wood PL, Jr, Anuar S, Riyanto A, Ahmad N, Muin MA, Sumontha M, Grismer JL, Onn CK, Quah ESH, Pauwels OSA (2014) Systematics and natural history of Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia. *Zootaxa* 3880: 1–147. <https://doi.org/10.1002/ece3.6961>
- Grismer LL, Wood PL Jr, Poyarkov NA, Le MD, Karunarathna S, Chomdej S, Suwannapoom C, Liu S, Che J, Quah ESH, Kraus F, Oliver PM, Riyanto, A, Pauwels OGS, Grismer JL (2021) Karstic landscapes are foci of species diversity in the world's third-largest vertebrate genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata: Gekkonidae). *Diversity* 13: 183, (5) <https://doi.org/10.3390/d13050183>
- Groth JG, Barrowclough GF (1999) Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* 12: 115–123.
- Harfoot MJB, Newbold T, Tittensor DP, Emmott S, Hutton J, Lyutsarev V, Smith MJ, Scharlemann JPW, Purves DW (2014). Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLoS Biology* 12, e1001841. <https://dx.doi.org/10.1371/journal.pbio.1001841>
- Harvey MS, Rix MG, Framenau VW, Hamilton ZR, Johnson MS, Teale RJ, Humphreys G, Humphreys WF (2011) Protecting the innocent: studying short-range endemic taxa enhances conservation outcomes. *Invertebrate Systematics* 25: 1–10. <https://doi.org/10.1071/IS11011>
- Heath TA, Hedtke SM, Hillis DM (2008) Taxon sampling and the accuracy of phylogenetic analyses. *Journal of Systematics and Evolution* 46: 239–257.
- Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522. <https://doi.org/10.1093/molbev/msx281>
- Holderegger R, Balkenhol N, Bolliger J, Engler JO, Gugeril F, Hochkirch A, Nowak C, Segelbacher G, Widmer A, Zachos FE (2019) Conservation genetics: linking science with practice. *Molecular Ecology* 28: 3848–3856. <https://doi.org/10.1111/mec.15202>
- Honda M, Ota H (2017) On the live coloration and partial mitochondrial DNA sequences in the topotypic population of *Goniurosaurus kuroiwaie orientalis* (Squamata: Eublepharidae), with description of a new subspecies from Tokashikijima Island, Ryukyu Archipelago, Japan. *Asian Herpetological Research* 8: 96–107. <https://doi.org/10.16373/j.cnki.ahr.170003>
- Honda M, Kurita T, Toda M, Ota H (2014) Phylogenetic relationships, genetic divergence, historical biogeography and conservation of an endangered gecko, *Goniurosaurus kuroiwaie* (Squamata: Eublepharidae), from the central Ryukyus, Japan. *Zoological Science* 31: 309–320. <https://doi.org/10.2108/zs130201>
- Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310–2314. <https://doi.org/10.1126/science.1065889>
- Jombart T, Devillard S, Balloux F. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics* 11: 94.
- Jonniaux P, Kumazawa Y (2008) Molecular phylogenetic and dating analyses using mitochondrial DNA sequences of eyelid geckos (Squamata: Eublepharidae). *Gene* 407: 105–115. <https://doi.org/10.1016/j.gene.2007.09.023>
- Kaatz A, Grismer JL, Grismer LL (2021) Convergent evolution in ecomorphology and habitat preference in Bent-toed Geckos (*Cyrtodactylus*) from Peninsular Malaysia *Vertebrate Zoology* in press.
- Kurita T, Honda M, Toda M (2008) Species delimitation and biogeography of the Ryukyu ground geckos, *Goniurosaurus kuroiwaie* ssp. (Squamata: Eublepharidae), by use of mitochondrial and nuclear DNA analyses. *Journal of Zoological Systematics and Evolutionary Research* 56: 209–222. <https://doi.org/10.1111/jzs.12198>
- Liang B, Zhou RB, Liu YL, Chen B, Grismer LL, Wang N (2018) Renewed classification within *Goniurosaurus* (Squamata: Eublepharidae) uncovers the dual roles of a continental island (Hainan) in species evolution. *Molecular Phylogenetics and Evolution* 127: 646–654. <https://doi.org/10.1016/j.ympev.2018.06.011>
- Leonart J, Salat J, Torres GJ (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology* 205: 85–93. <https://doi.org/10.1006/jtbi.2000.2043>
- Losos JB (2010) Adaptive radiation, ecological opportunity, and evolutionary determinism. *American Naturalist* 175: 623–639.
- Luo Z, Tang S, Jiang Z, Chen J, Fang H, Li C (2016) Conservation of terrestrial vertebrates in a global hotspot of karst in southwestern China. *Scientific Reports*. <https://dx.doi.org/10.1038/srep25717>
- Luu VQ, Bonkowski M, Nguyen TQ, Le MD, Schneider N, Ngo HT, Ziegler T (2016) Evolution in karst massifs, cryptic diversity among bent-toed geckos along the Truong Son Range with descriptions of three new species and one new country record from Laos. *Zootaxa* 4107: 101–140. <https://doi.org/10.11646/zootaxa.4107.2.1>
- Meiri S (2018) Traits of lizards of the world: variation around a successful evolutionary design. *Global Ecology and Biogeography* 2108: 1–5. <https://doi.org/10.1111/geb.12773>
- Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30: 1188–1195. <https://doi.org/10.1093/molbev/mst024>
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA pp. 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Mocquard F (1897) Notes herpétologiques. *Bulleton of the Museum of Natural History, Paris* 3: 211–217.
- Moritz C, Patton JL, Schneider CJ, Smith TB (2000) Diversification of rainforest faunas: an integrated molecular approach. *Annual Review*

- of Ecology and Systematics 31: 533–563. <https://doi.org/10.1146/annurev.ecolsys.31.1.533>
- Nakamura Y, Takahashi A, Ota H (2014) A new, recently extinct subspecies of the Kuroiwa's Leopard Gecko, *Goniurosaurus kuroiwa* (Squamata: Eublepharidae), from Yoronjima Island of the Ryukyu Archipelago, Japan Acta Herpetologica 9: 61–73. https://doi.org/10.13128/Acta_Herpetol-13269
- Nielsen SV, Oliver PM (2017) Morphological and genetic evidence for a new karst specialist lizard from New Guinea (*Cyrtodactylus*: Gekkonidae). Royal Society Open Science 2017 4 170781. <https://doi.org/10.1098/rsos.170781>
- Ngo HN, Nguyen TQ, Phan TQ, van Schingen M, Ziegler T (2019b) A case study on trade in threatened Tiger Geckos (*Goniurosaurus*) in Vietnam including updated information on the abundance of the endangered *G. catbaensis*. Nature Conservation 33: 1–19.
- Ngo HN, Le QT, Pham LM, Le MD, van Schingen M, Ziegler T (2019a) First record of the Cat Ba tiger gecko, *Goniurosaurus catbaensis*, from Ha Long Bay, Quang Ninh Province, Vietnam: microhabitat selection, potential distribution, and evidence of treats. Amphibian and Reptile Conservation 13: 1–13.
- Ngo HN, Ziegler T, Nguyen TQ, Pham CT, Nguyen TT, Le MD, van Schingen M (2016) First population assessment of two cryptic tiger geckos (*Goniurosaurus*) from Northern Vietnam: Implications for conservation. Amphibian and Reptile Conservation 10: 34–45
- Ngo HN, Nguyen HQ, Tran HM, Ngo HT, Le MD, Gewiss LR, van Schingen-Khan M, Nguyen TQ, Ziegler T (2021) A morphological and molecular review of the genus *Goniurosaurus*, including an identification key. European Journal of Taxonomy in press
- Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Nguyen TQ (2011) Systematics, ecology, and conservation of the lizard fauna in northeastern Vietnam, with special focus on *Pseudocalotes* (Agamidae), *Goniurosaurus* (Eublepharidae), *Sphenomorphus* and *Tropidophorus* (Scincidae) from this country. PhD thesis, University of Bonn, Bonn, Germany.
- Nguyen VS, Ho TC, Nguyen QT (2009) Herpetofauna of Vietnam. Edition Chimaira, Frankfurt am Main.
- Orlov NL, Ananjeva, NB, Nguyen TT (2020) New record and distribution of the genus *Goniurosaurus* Barbour, 1980 (Eublepharidae, Sauria, Reptilia) in Vietnam. Russian Journal of Herpetology 27: 179–184.
- Orlov NL, Ryabow SA, Nguyen TT, Nguyen QT, Ho TC (2008) A new species of *Goniurosaurus* (Sauria: Gekkota: Eublepharidae) from north Vietnam. Russian Journal of Herpetology 15: 229–244.
- Palumbi S, Martin A, Romano S, McMillan WO, Stice L, Grabowski G. (1991) The simple fool's guide to PCR. Version 2.0. University of Hawaii, Honolulu, pp 1–24.
- Paradis E, Schliep K (2018) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 1, 93.
- Qi S, Grismer LL, Lyu ZT, Zhang L, Li PP, Wang YY (2020a) A definition of the *Goniurosaurus yingdeensis* group (Squamata, Eublepharidae) with the description of a new species. ZooKeys 986: 127–155. <https://doi.org/10.3897/zookeys.986.47989>
- Qi S, Wang J, Grismer LL, Chen H-H, Lyu Z-T, Wang Y-Y (2020b) The Stoor Hobbit of Guangdong: *Goniurosaurus gollum* sp. nov., a cave-dwelling Leopard Gecko (Squamata, Eublepharidae) from South China. ZooKeys 991: 137–153. <https://doi.org/10.3897/zookeys.991.54935>
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. Available from: <http://www.R-project.org> (accessed 1 August 2018)
- Rambaut A, Drummond AJ (2014) TreeAnnotator v1. 7.0. <https://doi.org/10.1186/1471-2148-7-214>
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2014). Tracer v1.6. <https://doi.org/10.1093/sysbio/syy032>
- Reist JD (1986) A empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. Canadian Journal of Zoology 64: 1363–1368. <https://doi.org/10.1139/z86-203>
- Revell LJ (2012) Phytools: An R package for phylogenetic comparative biology (and other things), Methods in Ecology and Evolution 3: 217–223. <https://doi.org/10.1111/j.2041-210x.2011.00169.x>
- Rolland J, Cadotte MW, Davies J, Devictor V, Lavergne S, Mouquet N, Pavoine S, Rodrigues A, Thuiller W, Turcati L, Winter M, Zupan L, Jabot F, Morlon H (2012) Using phylogenies in conservation: new perspectives. Biology Letters 8: 692–694. <https://doi.org/10.1098/rsbl.2011.1024>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna B, Larget L, Liu L, Suchard MA, Huelsenbeck JP (2012) Mr. Bayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sgro CM, Lowe AJ, Hoffmann AA (2010) Building evolutionary resilience for conserving biodiversity under climate change. Evolutionary Applications. <https://doi.org/10.1111/j.1752-4571.2010.00157.x>
- Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans B, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila LJ, Morando M, De la Riva IJ, Sepulveda PV, Rocha CFD, Ibarguén-goyta N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, BranchWR, Clobert J, Sites Jr, JW (2006). Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894–899. <https://doi.org/10.1126/science.1184695>
- Sterling E J, Hurley MM, Le MD (2006). Vietnam: A natural history. New Haven, CT, London: Yale University Press.
- Stuart BL, Rhodin AG, Grismer LL, Hansel T. 2006. Scientific description can imperil species. Science 312: 1137. <http://dx.doi.org/10.1126/science.312.5777.1137b>
- Thorpe RS (1975) Quantitative handling of characters useful in snake systematics with particular reference to interspecific variation in the Ringed Snake *Natrix natrix* (L.). Biological Journal of the Linnean Society 7: 27–43. <https://doi.org/10.1111/j.1095-8312.1975.tb00732.x>
- Thorpe RS (1983) A review of the numerical methods for recognizing and analyzing racial differentiation. In: Felsenstein J (Ed.), Numerical Taxonomy. NATO ASI Series. Series G: Ecological Sciences. Vol. 1. Springer-Verlag, Berlin, pp. 404–423. https://doi.org/10.1007/978-3-642-69024-2_43
- Trifinopoulos J, Nguyen L-T, von Haesele A, Minh BQ (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44: W232–W235. <https://doi.org/10.1093/nar/gkw256>

- Turan, C (1999) A note on the examination of morphometric differentiation among fish populations: The Truss System. *Turkish Journal of Zoology*, 23, 259–263.
- Uetz, P, Hosek, J, eds. (2021) The Reptile database. <http://www.reptile-database.org> (accessed on 5 March 2021).
- Vane-Wright RI, Humphries CJ, Williams PH (1991) What to protect? systematics and the agony of choice. *Biological Conservation* 55: 235–254. [https://doi.org/10.1016/0006-3207\(91\)90030-D](https://doi.org/10.1016/0006-3207(91)90030-D)
- von Oheimb PV, von Oheimb KCM, Hirano T, Do VT, Luong HV., Ablett J, Phanm SV, Naggs (2017) Competition matters: Determining the drivers of land snail community assembly among limestone karst areas in northern Vietnam. *Ecology and Evolution* 28: 4136–4149. <https://doi.org/10.1002/ece3.3984>
- Vu, NT, Nguyen TQ, Grismer LL, Ziegler T (2006) First record of the Chinese Leopard Gecko, *Goniurosaurus luii* (Reptilia: Eublepharidae) from Vietnam. *Current Herpetology* 25: 93–95.
- Wainwright PC, Price SA (2016) The impact of organismal innovation on functional and ecological diversification. *Integrative and Comparative Biology* 56: 479–488.
- Wang YY, Yang JH, Grismer LL (2013) A new species of *Goniurosaurus* (Squamata: Eublepharidae) from Libo, Guizhou Province, China. *Herpetologica* 69: 214–226.
- Wiens JJ (1998) Does adding characters with missing data increase or decrease phylogenetic accuracy? *Systematic Biology* 47: 625–640.
- Wiens JJ, Morrill MC (2011) Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Systematic Biology* 60: 719–731. <https://doi.org/10.1093/sysbio/syr025>
- Wilcox TP, Zwickl DJ, Heath TA, Hillis, DM (2002) Phylogenetic relationships of the Dwarf Boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution* 25: 361–371. [https://doi.org/10.1016/S1055-7903\(02\)00244-0](https://doi.org/10.1016/S1055-7903(02)00244-0)
- Winter M, Devictor V, Schweiger O (2012) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology and Evolution* 28: 199–204. <https://doi.org/10.1016/j.tree.2012.10.015>
- Vázquez DP, Gittleman JL (1998) Biodiversity conservation: does phylogeny matter? *Current Biology* 8: R379–R381. [https://doi.org/10.1016/S0960-9822\(98\)70242-8](https://doi.org/10.1016/S0960-9822(98)70242-8)
- Vu NT, Nguyen TQ, Grismer LL, Ziegler T (2006) First record of the Chinese leopard gecko, *Goniurosaurus luii* (Reptilia: Eublepharidae) from Vietnam. *Current Herpetology* 25: 93–95.
- Williams PH, Humphries CJ, Vane-Wright RI (1991) Measuring biodiversity: taxonomic relatedness for conservation priorities. *Australian Systematic Botany* 4: 665–679. <https://doi.org/10.1071/SB9910665>
- Yang JH, Chan BP (2015) Two new species of the genus *Goniurosaurus* (Squamata: Sauria: Eublepharidae) from Southern China. *Zootaxa* 3980: 67–80. <https://doi.org/10.11646/zootaxa.3980.1.4>
- Zhou R, Wang N, Chen B, Liang B (2018) Morphological evidence uncovers a new species of *Goniurosaurus* (Squamata: Eublepharidae) from the Hainan Island, China. *Zootaxa* 4369: 281–291. <https://doi.org/10.11646/zootaxa.4369.2.8>
- Zhou R, Peng X, Hou M, Yuan F (2019) A new species of genus *Goniurosaurus*—*G. sinensis*. *Journal of Shihezi University (Natural Science)* 37: 549–556.
- Zhu XY, Chen GY, Román-Palacios C, Li Z, He ZQ (2020a) *Goniurosaurus gezhi* sp. nov., a new gecko species from Guangxi, China (Squamata: Eublepharidae). *Zootaxa* 4852: 211–222. <https://doi.org/10.11646/zootaxa.4852.2.6>
- Zhu XY, Shen CZ, Liu YF, Chen L, Li Z, He ZQ (2020b) A new species of *Goniurosaurus* from Hainan Island, China based on molecular and morphological data (Squamata: Sauria: Eublepharidae). *Zootaxa* 4772: 349–360. <https://doi.org/10.11646/zootaxa.4772.2.6>
- Ziegler T, Nguyen TQ, Schmitz A, Stenke R, Rösler H (2008) A new species of *Goniurosaurus* from Cat Ba Island, Hai Phong, Northern Vietnam (Squamata: Eublepharidae). *Zootaxa* 1771: 16–30. <https://doi.org/10.11646/zootaxa.1771.1.2>
- Zwickl DJ, Hillis DM (2002) Increased taxon sampling greatly reduces phylogenetic error. *Systematic Biology* 51: 588–598. <https://doi.org/10.1080/10635150290102339>